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AUTHOR(S):

NARITA, Tetsuya; NISIBULA, Mulimbwa; MIZUNO, Toshihiko

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VERTICAL DISTRIBUTION AND SEASONAL ABUNDANCE OF ZOOPLANKTERS IN LAKE TANGANYIKA

Tetsuya NARITA

Otsu Hydrobiological Station, Kyoto University

Nisibula MULIMBWA

Centre of Uvira, Institute of Scientific Research

Toshihiko MIZUNO

Laboratory of Biology, Osaka Aoyama College

ABSTRACT Vertical distribution and seasonal abundance of zooplankters were studied in Lake Tanganyika. Faunal composition of zooplankton was simple. *Limnocyclus tanganyicae*, copepod nauplii, *Diaptomus simplex*, cyclopoids, and shrimp were collected by closing nets. Nauplii were dominant in number, but cyclopoid copepodites were dominant in biomass. The biomass calculated was in the range of 1.2-3.7 (average 2.3) g/m² excluding shrimp and medusa. For the vertical distribution of the copepods, the larger the size, the deeper the layers they stayed in the daytime, and the more remarkable diel vertical migration they showed. Chlorophyll *a* amount was high at the end of September and in October, which coincides with the bloom of *Anabaena* and *Dictyosphaerium* off Myako. The time of phytoplankton bloom off Myako seemed to correspond with that of other parts of the lake as cited in the literature. The number of *Diaptomus* females with eggs increased in September and October, and the number of shrimp also increased in October. The increase of *Diaptomus* females with eggs corresponded with phytoplankton abundance. The seasonal abundance and high reproduction of zooplankters seemed to be a product of the abundance of phytoplankton in Lake Tanganyika.

INTRODUCTION

Descriptions of zooplankton species of Lake Tanganyika have been made by Sars (1909), Gurney (1928), and Lindberg (1951) on Copepoda, Harding (1957) on Cladocera, and Rousset (1910), Beauchamp (1932) and Gillard (1957) on Rotifera.

The absence or scarcity of cladocerans and rotifers in the open water and the richness of endemic cyclopoids have been noticed to be the characteristics of zooplankton in this lake (Cunnington, 1920; Lindberg, 1951). Despite this unique character of composition, only a few studies have been made from an ecological viewpoint.

Hecky et al. (1981) pointed out that the fish yield was unusually high relative to the rate of primary production of phytoplankton. Zooplankton must play an important role in transferring energy for fish with high production. Burgis (1984) estimated high transfer efficiency from primary production to zooplankton production in the lake. Knowledge about the distribution, abundance and production of zooplankters of the lake are essential for understanding the lake ecosystem.

In the present study vertical distribution and seasonal change of abundance of zooplankters in Lake Tanganyika will be shown, and seasonality of the reproductive activity of zooplankters led by the phytoplankton abundance will be described.

STUDY AREA, MATERIALS AND METHODS

The first author worked 2 km off Myako, Mahale Peninsula, on the central part of the east

coast of the lake, in Tanzania from July to November in 1981. The second author collected zooplankton 2 km off Uvira, on the northwest end of the lake, in Zaire from September 1981 to August 1982. Zooplankton collected by Dr. M. Hori off Uvira in 1979 were also used to show the vertical distribution of zooplankters by day and at night.

Water Temperature: Off Myako, water temperatures were measured twice vertically with Hg-thermometer set in a 3-liter Van Dorn type water sampler. Off Uvira, an alcohol thermometer set in a water bottle was used for the measurements.

Chlorophyll a: Four to six liters of water from each depth above 100 m were filtered through a Whatman GF/C filter at Myako. The filters were kept in a box with silica gel under dark in room temperature conditions. Chlorophyll *a* was analyzed by the UNESCO method and pheopigments of some filters were analyzed by the Lorenzen method in Japan.

Phytoplankton: At Myako, 200 ml of water each from 1, 5, 10, and 20 m depth were mixed in a 1-liter bottle and Lugol solution was added. After sedimentation, 4 subsamples of 0.0009 ml out of a concentrated sample (1–2 ml) were examined using a haematocytometer. The mean density of phytoplankters was calculated into the number per 1 ml of mixed water.

Zooplankton: At Myako the collections were made in the morning (09:00–11:00) and at night (21:00–23:00) by a closing net with a mouth of 24 cm in diameter and mesh of 70 μ m aperture. The samples were fixed with Lugol solution and preserved with about 4% formalin afterwards. Two 1 ml subsamples out of a concentrated sample of 20–30 ml were examined. When zooplankton were scarce, all animals in the sample were counted. All medusa and shrimp were counted separately for each sample.

At Uvira, the collections were made with a closing net with 24 cm diameter at mouth and 100 μ m in mesh. Four 0.1 ml subsamples were counted for each sample.

RESULTS AND DISCUSSION

Water Temperature

Off Myako the temperature was found to gradually decrease with depth (Fig. 1A). Difference between the temperatures of 1 m and 100 m deep was 3°C at the most. The temperatures at the 1 m layer varied with a range of 25.6°C on August 11 to 27.3°C on October 12, but those at the 50 m and 100 m layers were fairly constant, remaining at about 25 and 24°C respectively, during the 4 month period (Fig. 1A).

Off Uvira, isothermal water down to 100 m deep appeared in June and July, while in other months the vertical distribution pattern of temperature was quite similar to that off Myako (Fig. 1B). The isothermal water down to 100 m deep may have been brought about by vertical mixing due to the strong Southeast Trade Wind from June to September. Such a phenomenon has been reported in both the northern and southern end of the lake (Dubois, 1958; Coulter, 1963).

General trends of seasonal change in the vertical distribution of temperature off Myako and Uvira consistent with those of other parts of the lake. Seasonal variation of the temperature off Myako in the open lake conditions, is fairly small compared to both ends of the lake.

Transparency

Secchi disk transparency generally fell between 10 and 14.5 m, except for 7.0 m on Septem-

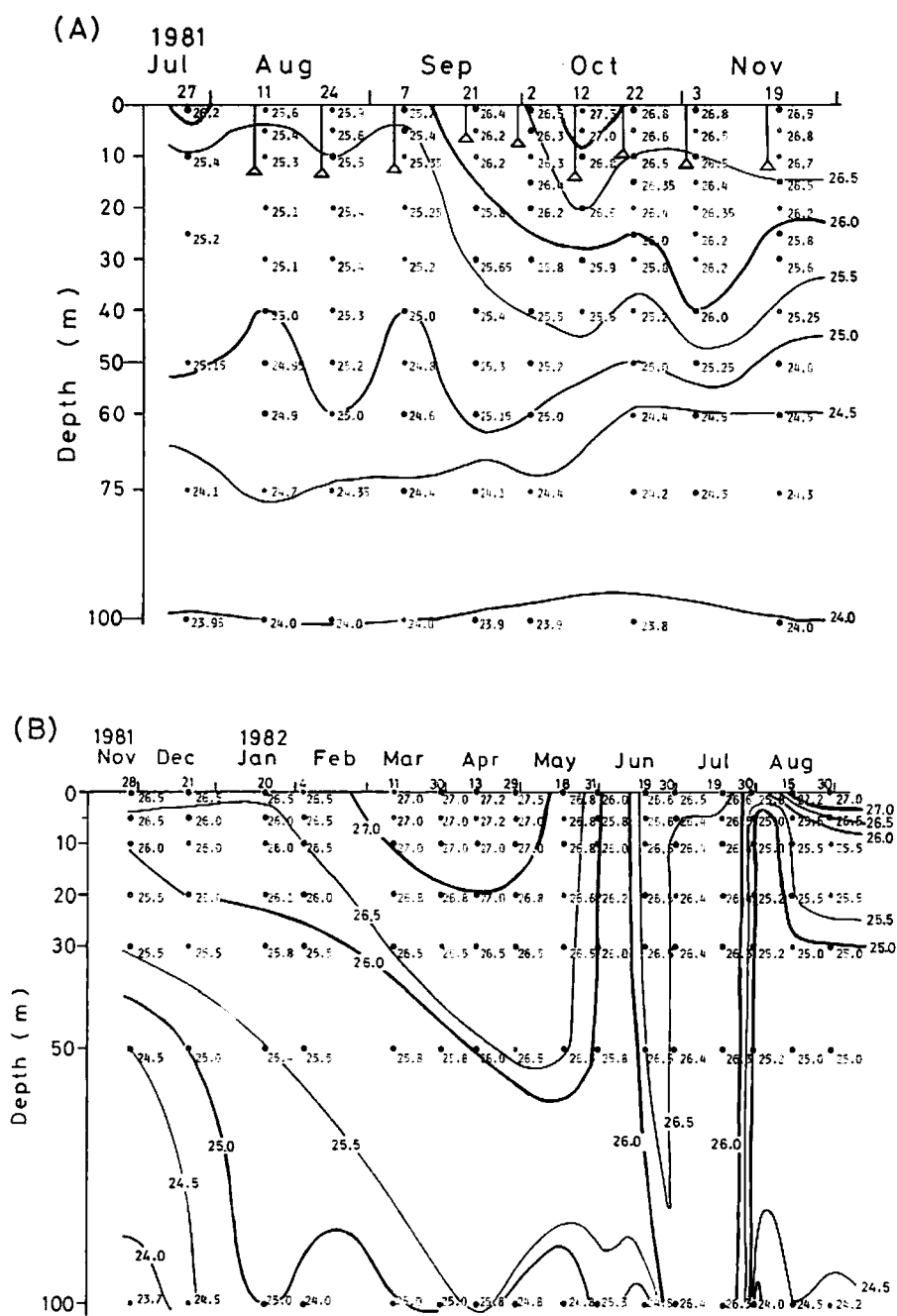


Fig. 1. (A) Isotherms of water temperature and transparency off Myako from July to November 1981, (B) isotherms off Uvira from November 1981 to August 1982.

ber 21 and 8.0 m on October 2 off Myako (Fig. 1A). Extinction coefficients ($k = 1.9/\text{Tr}$, Ichimura, 1956) was estimated to be 0.19–0.13 (l/m), and the photic zone depth (a depth of 1 % of the surface light intensity; roughly estimated using the values of k and the Lambert-Beer law) was 24–35 m. On September 21 and October 2, the extinction coefficients were 0.27 and 0.24, and the depth of the photic zone were 17 and 19 m, respectively. Such relatively low transparencies have been observed in various other parts of the lake including its northern and southern extremes (Dubois, 1958; Coulter, 1963; Hecky et al., 1978).

Phytoplankton

Large sized phytoplankters found off Myako were as follows. Among Cyanophyta, *Aphanocapsa delicatissima*, *Anabaenopsis tanganikae* and *Anabaena* sp. (*flos-aquae*?), in Chlorophyta, *Sphaerocystis shroeteri*, *Oocystis lacustris*, *O. borgei*, *Dictyosphaerium pulchellum*, *Dimorphococcus lumatus*, *Coelastrum cambricum*, *Scenedesmus* spp. and *Crucigenia rectangularis*, and in Diatomae, *Nitzschia asterionelloides*, *N. nyassensis*, *Navicula gastrum* and *Ropadalia* sp. were identified.

Succession in the phytoplankton community during the study period was characterized by alternative propagation of *Nitzschia* and *Anabaena* (Fig. 2). There was almost no *Anabaena* before September 21, but very abundant, and in bloom on September 21 and October 2, and decreasing thereafter. *Dictyosphaerium* increased on the same days as the *Anabaena* bloom and showed its peak on October 2. On the contrary, *Nitzschia* decreased suddenly on August 24 and was scarce until the middle of October when *Anabaena* and *Dictyosphaerium* were predominant. As they descended, *Nitzschia* again became predominant. The colony number of *Sphaerocystis* did not change much, and *Anabaenopsis tanganikae* was common throughout the period.

Coulter (1963) found a great abundance of phytoplankton in July and September, and also secondary bloom in November and December at the southern end of the lake. The bloom of *Anabaena flos-aquae* in September and/or in October have been found in the northern basin

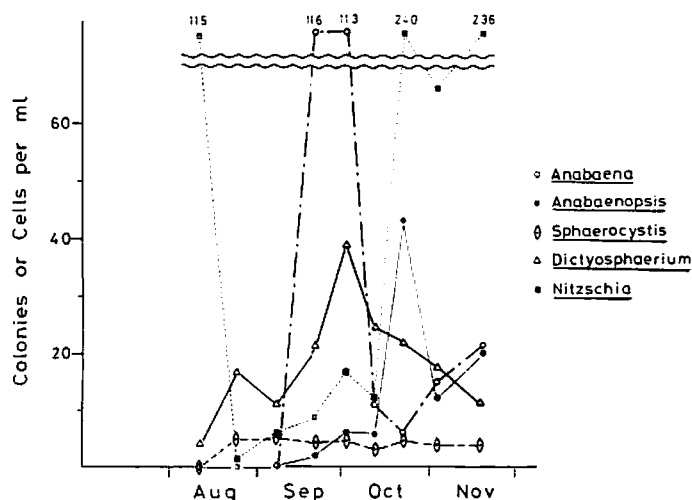


Fig. 2. Number of colonies (n/ml) of dominant large sized phytoplankters in the mixed water of 200 ml each from 1, 5, 10, and 20 m deep off Myako from August to November 1981. (cell number for *Nitzschia*)

of the lake by Van Meel (1954), Symoens (1956), Dubois (1958) and Hecky et al. (1978). Although the timing and the subdominant species in bloom vary slightly depending on the year and the locality in the lake, the onset of bloom of *Anabaena* after the windy dry season seems to be a common phenomenon in the seasonal succession of phytoplankton in this lake.

Chlorophyll *a*

The maximum chlorophyll *a* amount of 5.6 $\mu\text{g/l}$ was obtained at the 1 m layer on September 21 (Fig. 3), when *Anabaena* bloom was seen on the lake surface. Except for blooming time (September 21 and October 2), the amount of chlorophyll *a* was usually very low (less than 2 $\mu\text{g/l}$) and the chlorophyll peak was usually observed at around the 10 m layer during this period.

Using the fluorescent method Hecky and Kling (1981) reported that the average chlorophyll *a* amount at the 0.5 m layer in the pelagic area was 0.3 $\mu\text{g/l}$ in May, and 5.2 $\mu\text{g/l}$ in October. In the present study, the average chlorophyll *a* amount at the 1 m layer was 0.78 $\mu\text{g/l}$ during the period excluding the blooming time, and more than double Hecky and Kling's value. The UNESCO method which overestimates the chlorophyll *a* amount by including some pheo-

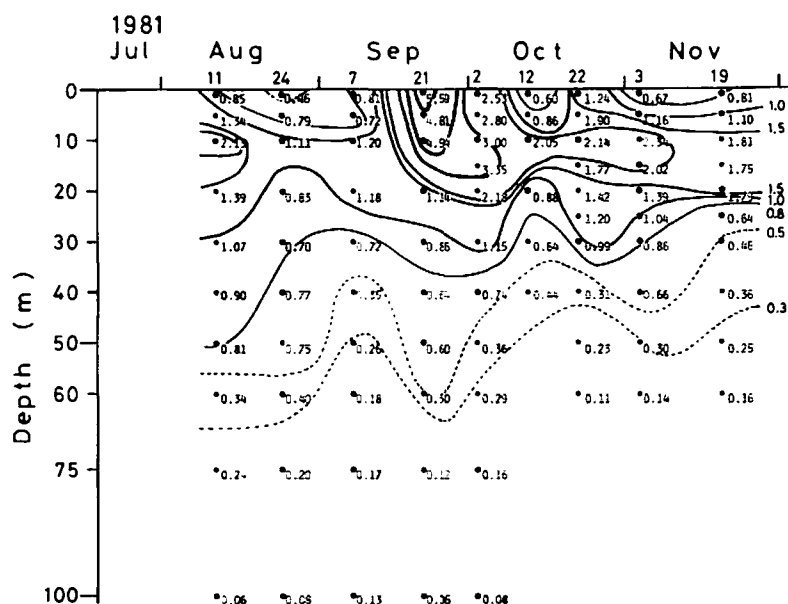


Fig. 3. Chlorophyll *a* distribution off Myako from July to November 1981.

Table 1. Chlorophyll of total phytoplankton and of smaller than 25 μm phytoplankton, and its ratio.

	Total	<25 μm	<25 μm /total
1 m	0.80 $\mu\text{g}\cdot\text{l}^{-1}$	0.58 $\mu\text{g}\cdot\text{l}^{-1}$	73 %
5	1.08	1.00	93
10	1.27	1.05	83
20	0.94	0.83	88
30	0.70	0.76	109

pigments (Nakanishi, per. comm.) in addition to the spatial and temporal variation of phytoplankton abundance might be partly responsible for the difference between Hecky and Kling's value and ours. The percentage of pheopigments to chlorophyll *a* plus pheopigments, analyzed by the Lorenzen method, were 5–48% (average 20%) at the 1 m layer, increasing with depth in the photic zone.

The chlorophyll *a* amount in the algal fraction smaller than 25 μm by netting were more than 73% of the total chlorophyll *a* on August 31 (Table 1). But, the percentage of the small fraction at bloom was not examined.

Zooplankton Fauna

The zooplankton composition in the pelagic area off Myako was simple. It consisted of protozoans, *Limnocyclus tanguensis*, copepod nauplii, *Diaptomus simplex*, cyclopoid copepods

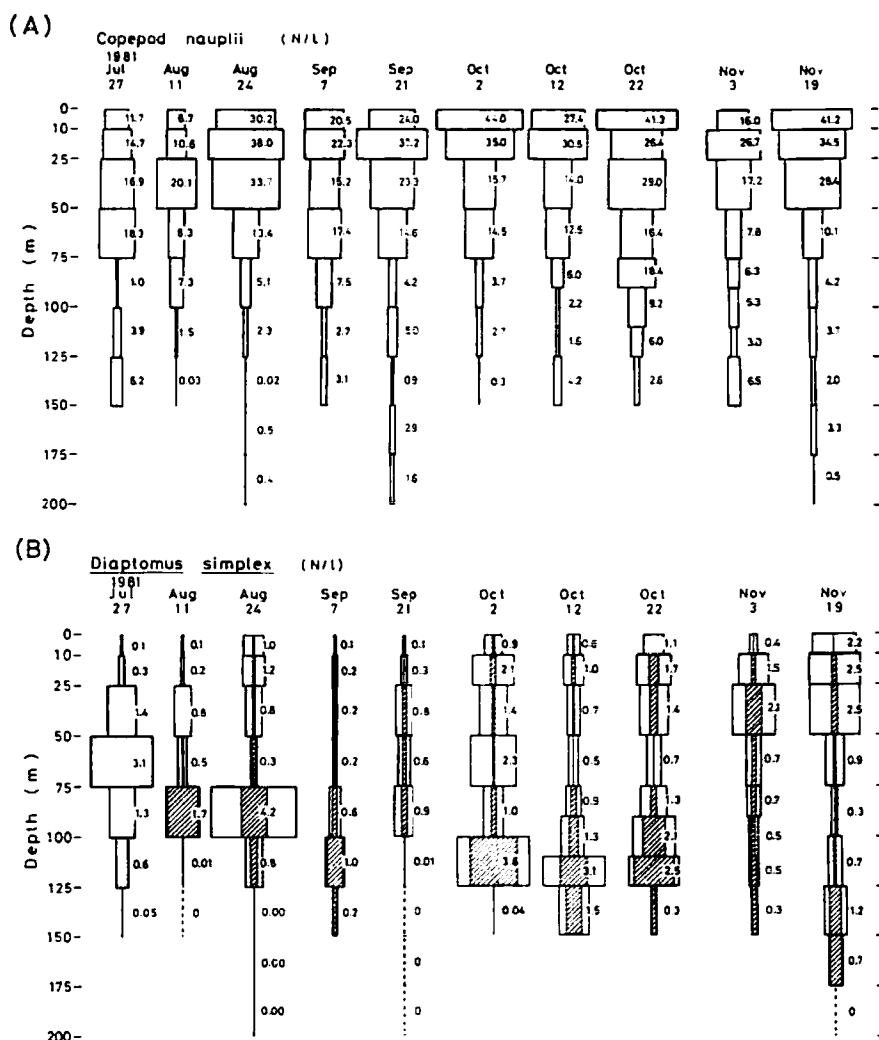


Fig. 4. Vertical distribution of zooplankters off Myako in the daytime from July to November 1981. (A) copepod nauplii, (B) copepodites and adults (shaded) of *Diaptomus simplex*.

and shrimp. Colonies or single cells of *Vorticella* sp. were always found, but they were not counted. Only one rotifer, *Asplanchna* sp., was found in the 10–25 m sample on October 2, and no cladoceran was found in any samples. The cyclopoids found were mostly in immature stages. Adult specimens identified were mainly *Mesocyclops leuckarti* and a few *Thermocyclops* sp. According to Lindberg (1951), *Mesocyclops leuckarti* and *Thermocyclops schuurmanae* were predominant among cyclopoids in open water. A few individuals of *Ergasiloides* were also found in the pelagic samples. The shrimp have not yet been identified.

Identification of seasonal samples of zooplankton off Uvira were not comparable to taxa off Myako.

Vertical distribution of zooplankters

Fig. 4 shows the vertical distribution of zooplankters off Myako collected in the daytime about every two weeks.

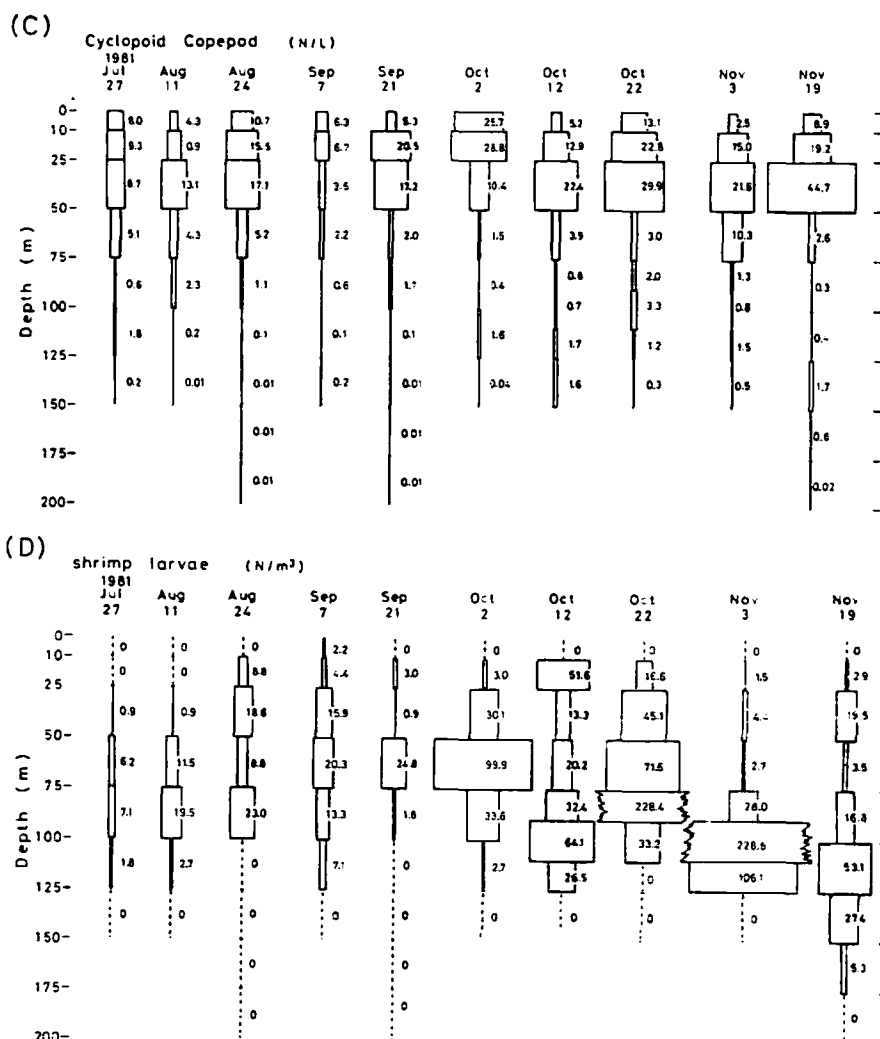


Fig. 4. (C) cyclopoids copepodites including adults, (D) shrimp.

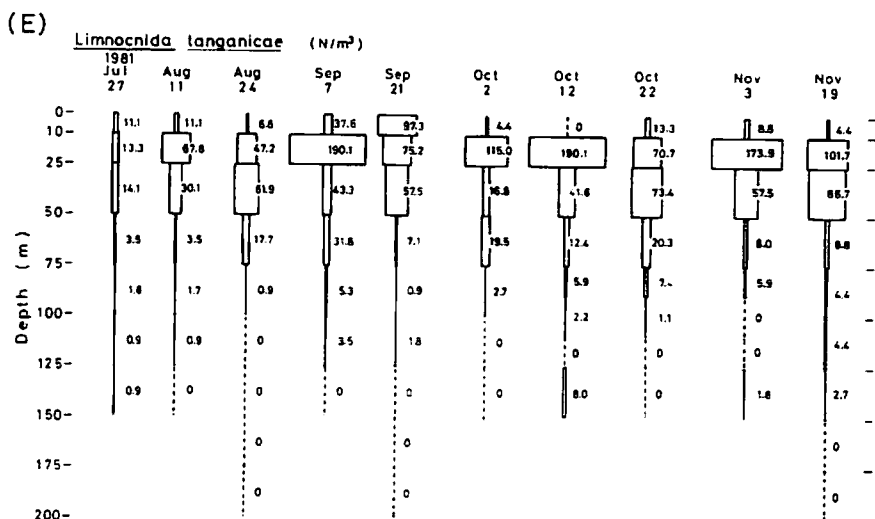


Fig. 4. (E) *Limnocyclus tanganicae*.

In the daytime, copepod nauplii were distributed mostly in the layers of 0–10 m and 10–25 m, but were few in the layers deeper than 75 m. A small number of nauplii were observed even in the sample from water at the 175–200 m layer. However it was in doubt whether they had been alive or dead. Judging from the scarcity of live higher stages of *Diaptomus* and cyclopoids copepodites in the 175–200 m layer, the nauplii in that water are considered to be sinking dead specimens. Younger stages of *Diaptomus* copepodites were abundant in the water of 10–50 m, but adults were distributed in the 75–125 m layers (Figs. 4B and 5A). Cyclopoid copepodites were distributed mainly in the layers of 25–50 m and 10–25 m, being very scarce below 75 m. Higher stages of cyclopoid copepodites including adults were also more abundant in the water below 75 m than in the upper waters. For copepods, as a whole, the nauplii were in the upper portion of the water column, copepodites were in the mid portion, and adults were in the lower portion around 100 m in depth. The larger the size, the deeper the layer they were distributed in the daytime.

The shrimp were distributed mostly in the layers between 50–125 m, and were rather scarce in the upper layers of 0–25 m except for October 12, in the daytime (Fig. 4D). In October and November when they were abundant, the centre of their distribution was seen between 50–90 m, and none were collected below 125 m except on November 19. *Limnocyclus* was scarce in 0–10 m and was seen mostly in the layers of 10–50 m, and was almost completely absent below 75 m.

The lower boundary of distribution of zooplankters, especially *Diaptomus* and shrimp, was around 125 m, below which the zooplankters were very scarce. This boundary relates possibly to low oxygen water which appears in the 100–200 m layer in this lake (Beauchamp, 1939; Dubois, 1958; Coulter, 1963; Beadle, 1981).

Zooplankton distribution at night off Myako and off Uvira are similar (Fig. 6). Off Myako, the patterns of vertical distribution of nauplii at night were not different from that of the daytime. The cyclopoids moved slightly upward at night. *Diaptomus* copepodites moved upward into the upper layers at night (Figs. 5 and 6). The shrimp and *Limnocyclus* also migrated into the upper layers at night. Off Uvira, *Diaptomus* and cyclopoids also showed marked diel vertical migration (Figs. 6C and 7).

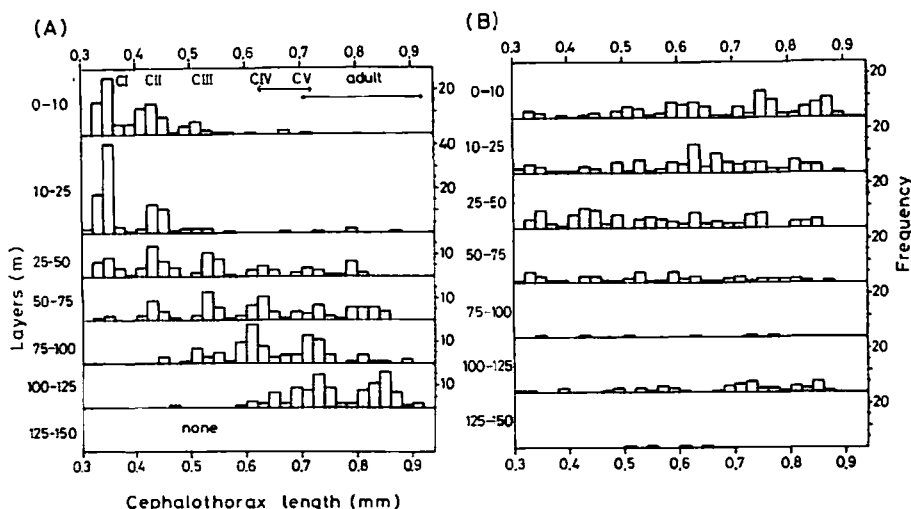


Fig. 5. Size frequency of *Diaptomus* copepodites in different layers off Myako in the day of August 24 (A) and the night of August 25 (B), 1981.

The diel vertical migration of *Diaptomus* and shrimp was most remarkable. These larger sized zooplankters moved down to the regime of deep water in the daytime, where it was low in both light intensity and phytoplankton density, and coming up to the epilimnion at night where phytoplankton was abundant. Their diel up and down long distance migration was probably due to their avoidance of strong predation by pelagic fishes, Ndagalas, in the daytime (Coulter, 1963).

Seasonal Change in the Number and Biomass of Zooplankters

Off Myako, the average percentage of the number of each taxon to total zooplankton under 1 m² from 0 m to 150 m was 62.4% for copepod nauplii, 5.2% for *Diaptomus* copepodites and

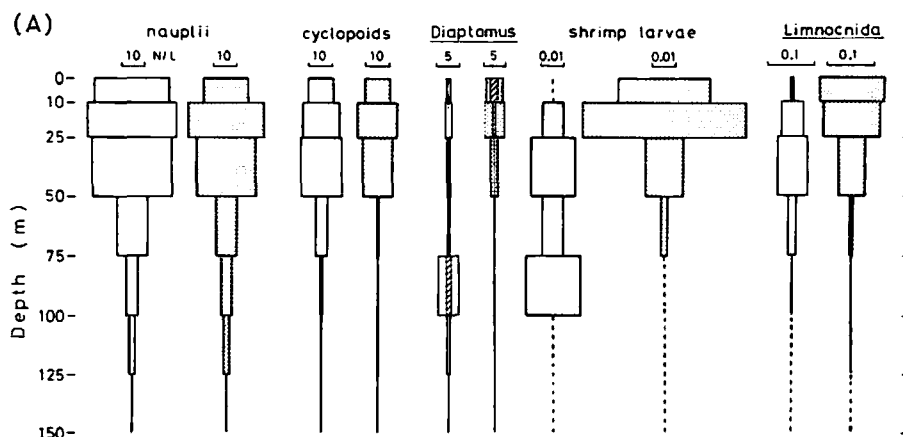


Fig. 6. Vertical distribution of zooplankters in day and at night. (A) Aug. 24 (day) and Aug. 25 (night) off Myako.

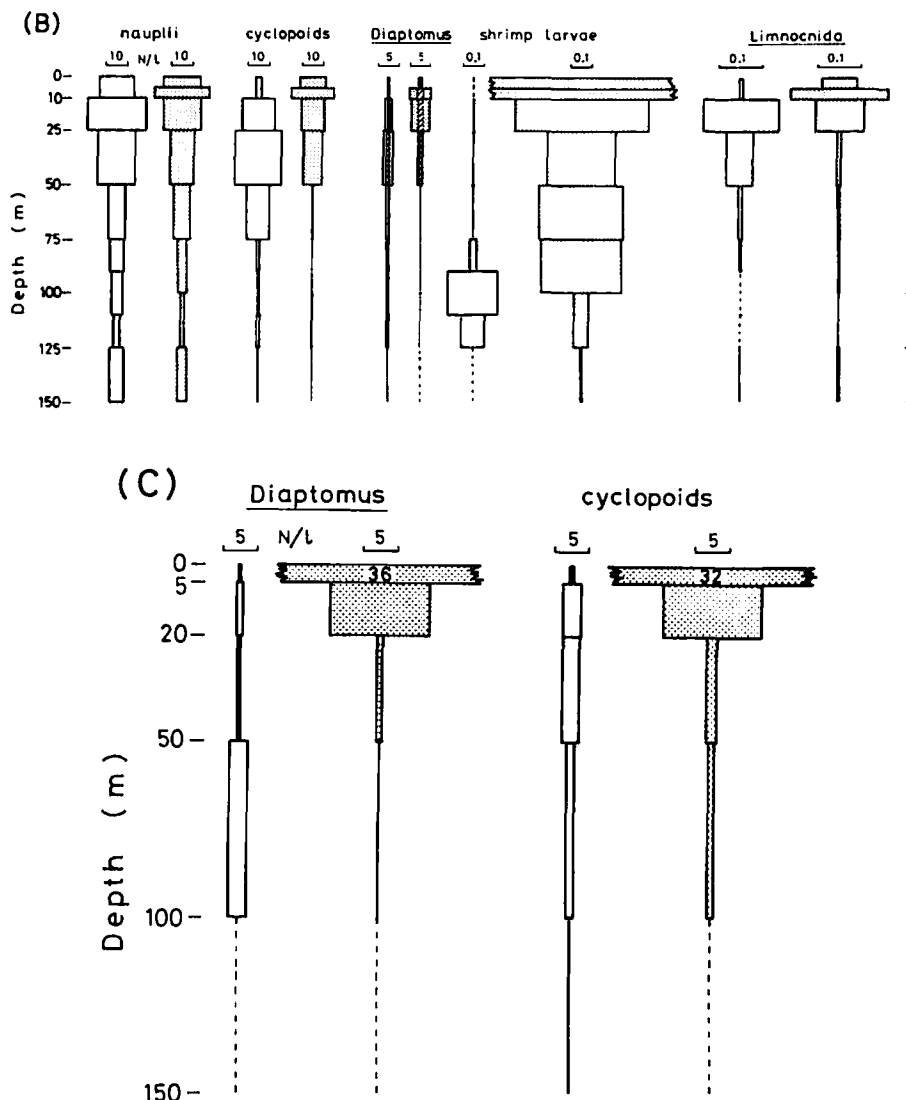
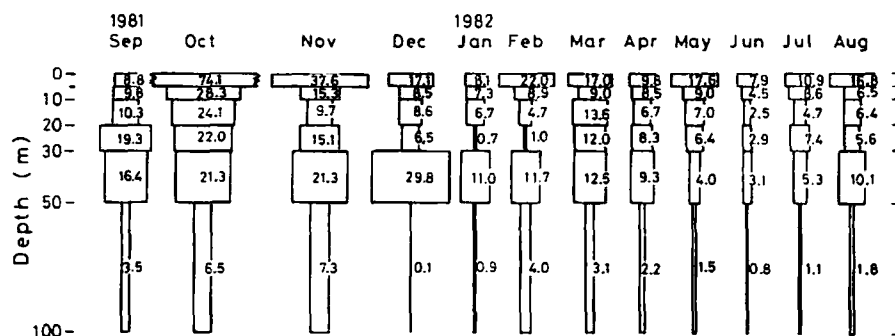


Fig 6. (B) Nov. 3 (day) and Oct. 31 (night) off Myako, (C) day and night of Oct. 30, 1979 off Uvira. open: day, shaded: night.

adults, 32.3% for cyclopoid copepodites and adults, 0.16% for *Limnocoidea* and 0.42% for shrimp. More than 50% was always occupied by nauplii, while the number of *Diaptomus* was fairly small. Cyclopoid copepodites were very abundant, although the cyclopoid adults were not.

Dry weight biomass of the copepods was estimated from the numbers of each taxon assuming the individual dry weight as follows; 0.3 μg for nauplii, 0.4 for large nauplii, 2.6 for *Diaptomus* copepodites, 4.5 for *Diaptomus* adults, 1.5 for cyclopoid copepodites, and 4.0 for cyclopoid adults (Schindler and Noven, 1971; Bottrell et al., 1976). The total copepod biomass

(A) Copepods (N/L)



(B) Eggs of Copepods (N/L)

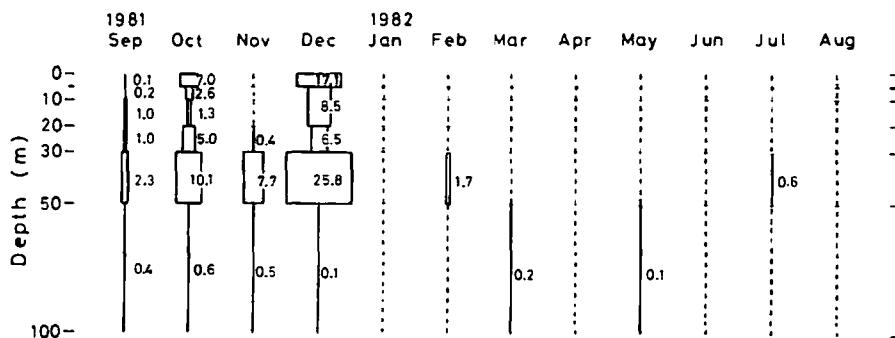
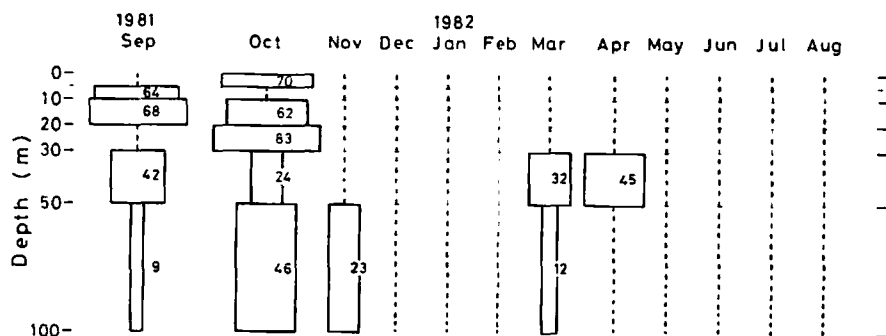
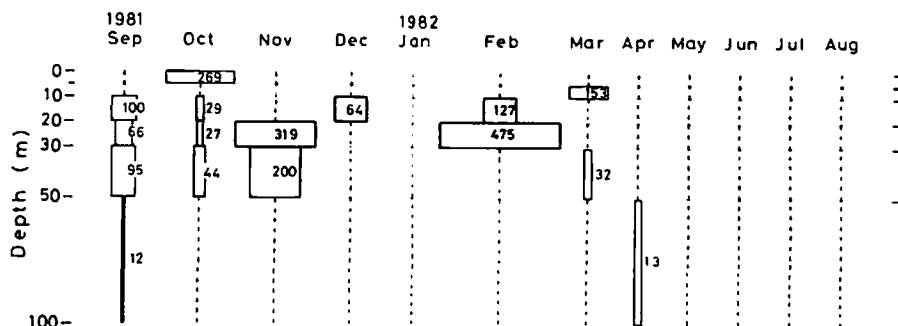
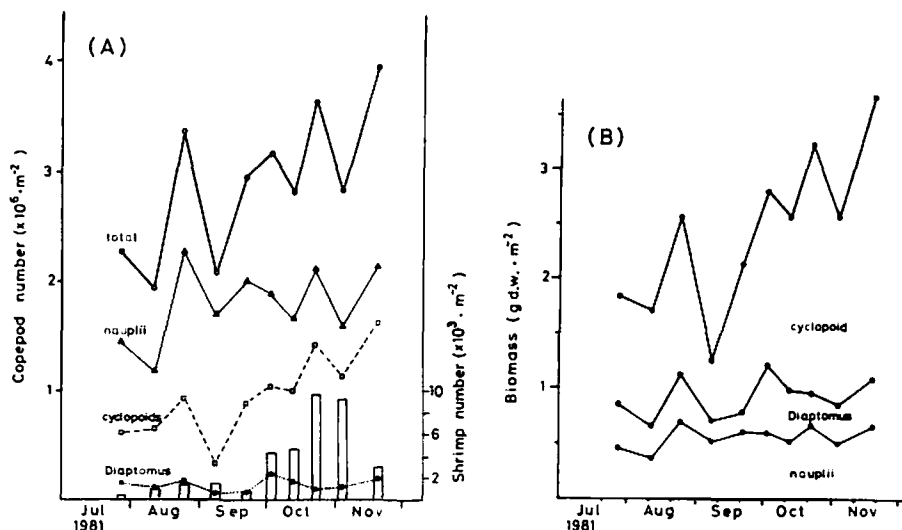
(C) Shrimp larvae (N/m³)

Fig. 7. Vertical distribution of zooplankton off Uvira from September 1981 to August 1982. (A) copepods, (B) copepods eggs, (C) shrimp.

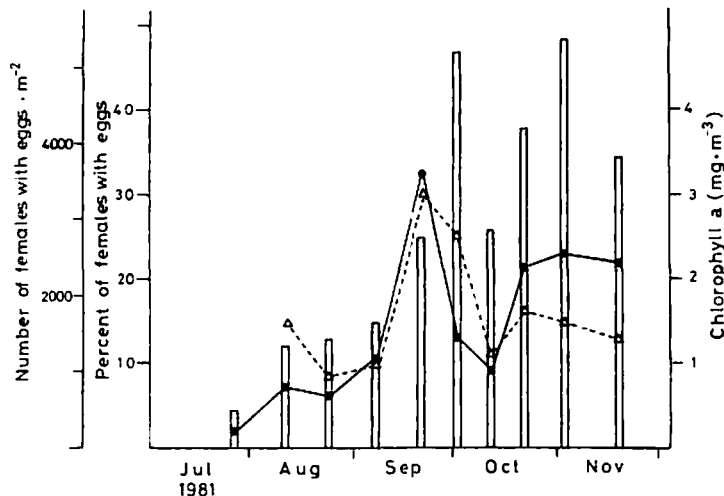
(D) *Limnocyclus tanagericae* (N/m³)Fig. 7. (D) *Limnocyclus tanagericae*.Fig. 8. Seasonal change of (A) number and (B) biomass of nauplii, *Diaptomus* copepodites and adults, cyclopoids, and shrimp (histogram) under 1 m² between 0-150 m off Myako.

was 1.2-3.7 g/m² (average 2.3) and tended to increase in October and November (Fig. 8B). Average shares of the biomass of each taxon to the total copepod biomass were 22.8, 16.2 and 60.0% for nauplii, *Diaptomus* copepodites and adults, and cyclopoid copepodites and adults, respectively.

According to Schindler (1969), a large part of the crustacean zooplankters can escape from the net at sampling, causing underestimation of the number of zooplankters. The average efficiency of catch with a net (70 μ m aperture) was 30% for nauplii and about 50% for *Mesocyclops leuckarti* and *Eodiaptomus japonicus* compared to those caught with a Patalas-Schindler transparent zooplankton trap in Lake Biwa (Narita, unpublished). As the correction was not made for net sampling in the present study, the true biomasses may be, at least, double the values obtained.

Table 2. Comparison of the zooplankton biomass in Lake Tanganyika with those in the pelagic water column of tropical and temperate lakes.

	Depth (m)	Dry weight g m ⁻²	Biomass g m ⁻³		
Tropical lakes					
George	2.25	0.48	0.21	Crust. zoopl.	Burgis et al. (1974)
Chad	2.5	0.30–0.98	0.12–0.39	all zoopl.	Saint-Jean (1983)
Lanao	60	15.8	0.26	copepods	Lewis (1979)
Tanganyika	(100)	4.8 (0.32–12.54)	0.048	all zoopl.	Burgis (1984)
"	(150)	2.3 (1.2–3.7)	0.015	copepods	present study
Temperate lakes					
Superior	148		0.017	crust. zoopl. (summer)	Patalas (1975)
Ontario	86		0.175	"	"
Huron	59		0.068	"	"
Erie	18–24		0.28–0.38	"	"

Fig. 9. Number of females with eggs (histogram), and percentage of females with eggs to total adult females (solid line) in *Diaptomus simplex*, and chlorophyll *a* amount under 1 m² between 0–20 m (broken line) off Myako.

The zooplankton biomass in the present study was comparable to that of Burgis (1984). But the biomasses per m³ in Lake Tanganyika are one order of magnitude less than those in other tropical and large temperate lakes, but were comparable to those in Lake Superior and Lake Huron (Table 2).

Off Myako, total copepod numbers were high after September, due to the increase in the number of cyclopoids (Fig. 8A), while the nauplii and *Diaptomus* did not increase. The shrimp also increased markedly in October and November (Fig. 8A). In the *Diaptomus* population, a clear increase in copepodites including adults was not detected except for a small peak on October 2 (Fig. 8A), but adult females with eggs increased from the end of September, and

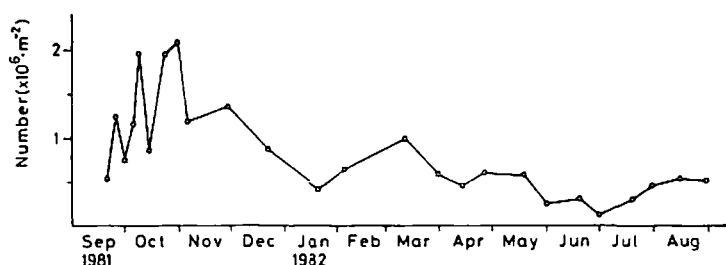


Fig. 10. Seasonal change of copepod number under 1 m² between 0-100 m off Uvira.

the percentage of egg-bearing females among all adult females was also high after September, with a peak on September 21 (Fig. 9). However, an expected increase of *Diaptomus* copepodites and adults following to the high number of reproductive females did not last past the end of September except for a small peak on October 2.

Off Uvira, as the copepods were not distinguished into nauplii, *Diaptomus* and cyclopoids, it was impossible to make close comparison with those off Myako. However, the number of copepods in October was particularly large (Fig. 10), as was the number of copepod eggs from September to December (Fig. 7B). This coincides well with the increasing number and frequency of reproductive females in the *Diaptomus* population off Myako. Shrimp was also abundant from September to November, which also corresponded with the population increase off Myako. These facts suggest that the reproduction of *Diaptomus*, shrimp, and possibly cyclopoids, were high both off Myako and off Uvira between September and October. According to Hecky and Kling (1981), the phytoplankton biomass off Bujumbura (near Uvira) is high between September and October. The increase in the numbers of copepods and shrimp off Myako and Uvira seems to correspond with high phytoplankton biomass. In Lake Tanganyika, thus, the abundance and reproduction of the zooplankters vary with the change of phytoplankton abundance.

In Lake George, the peaks of total copepod number coincide with the peaks of chlorophyll *a*, though the change in the number of zooplankters is small, only two-fold, in comparison to temperate lakes. The daily recruitments of *Thermocyclops hyalinus* from egg to nauplii is high, about two-fold, in October after the peak of chlorophyll in September, though the recruitments from nauplii to copepodites and from copepodites to adults do not follow the high recruitments from eggs to nauplii (Burgis, 1971). Reproduction of the zooplankters in oligotrophic Lake Tanganyika, where phytoplankton abundance is low and varies in large amplitudes, may change to a larger extent than that in eutrophic Lake George where phytoplankton biomass is high and changes less amplitudes. In Lake Tanganyika, as is in other tropical lakes with year-round high water temperature, reproduction of zooplankters is probably continuous. However, in this lake reproductive activity may not be constant throughout a year, varying according to the abundance of the phytoplankton, though to a lesser extent than in temperate lakes.

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Authors' Names and Addresses: Tetsuya NARITA, *Otsu Hydrobiological Station, Kyoto University, 4-1-23 Shimo-sakamoto, Otsu 520-01, Japan*; Nisibula MULIMBWA, *Institut de Recherche Scientifique/Uvira, Sud-Kivu, Zaire*; Toshihiko MIZUNO, *Laboratory of Biology, Osaka Aoyama College, 2-11-1 Niina, Minoo 562, Japan*.